

A NEW RHYNCHOSAUR FROM THE UPPER TRIASSIC OF WEST TEXAS, AND THE BIOCHRONOLOGY OF LATE TRIASSIC RHYNCHOSAURS

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ABSTRACT. A new rhynchosaur (Reptilia, Diapsida), *Otschalkia elderae*, from the lower Dockum Group of West Texas is represented by two premaxillary fragments, two femora, and two humeri. The lower Dockum is early late Carnian (*Paleorhinus* biochron) in age. Other Late Triassic rhynchosaurs are: indeterminate hyperodapedontines from the Popo Agie Formation of Wyoming, Isalo II beds of Madagascar and an undescribed stratigraphic unit in Tanzania; *Scaphonyx* from the Wolfville Formation of Nova Scotia, Santa Maria, and Caturrita Formations of Brazil and the Ischigualasto Formation of Argentina; *Hyperodapedon* from the Maleri Formation of India and the Lossiemouth Sandstone Formation of Scotland. These occurrences of Late Triassic rhynchosaurs are of early late Carnian age. Late Triassic rhynchosaur distribution is largely controlled by the facies that are preserved at different localities. Rhynchosaurs are common in more terrestrial faunas that contain few or no phytosaurs, whereas rhynchosaurs are rare in semiaquatic faunas dominated by phytosaurs.

RHYNCHOSAURS are an order of primitive archosauromorph reptiles whose fossils are found in Upper Triassic strata on all continents except Antarctica and Australasia (Benton 1987; Text-fig. 1) as well as in Lower and Middle Triassic strata (Benton 1990). Several authors have mentioned the presence of rhynchosaurs in the Late Triassic of North America (Baird 1964; Elder 1978; Chatterjee 1980; Benton 1983*b*, 1987; Murry 1989; Parrish 1989*a*, 1989*b*), but none of these specimens has been adequately described.

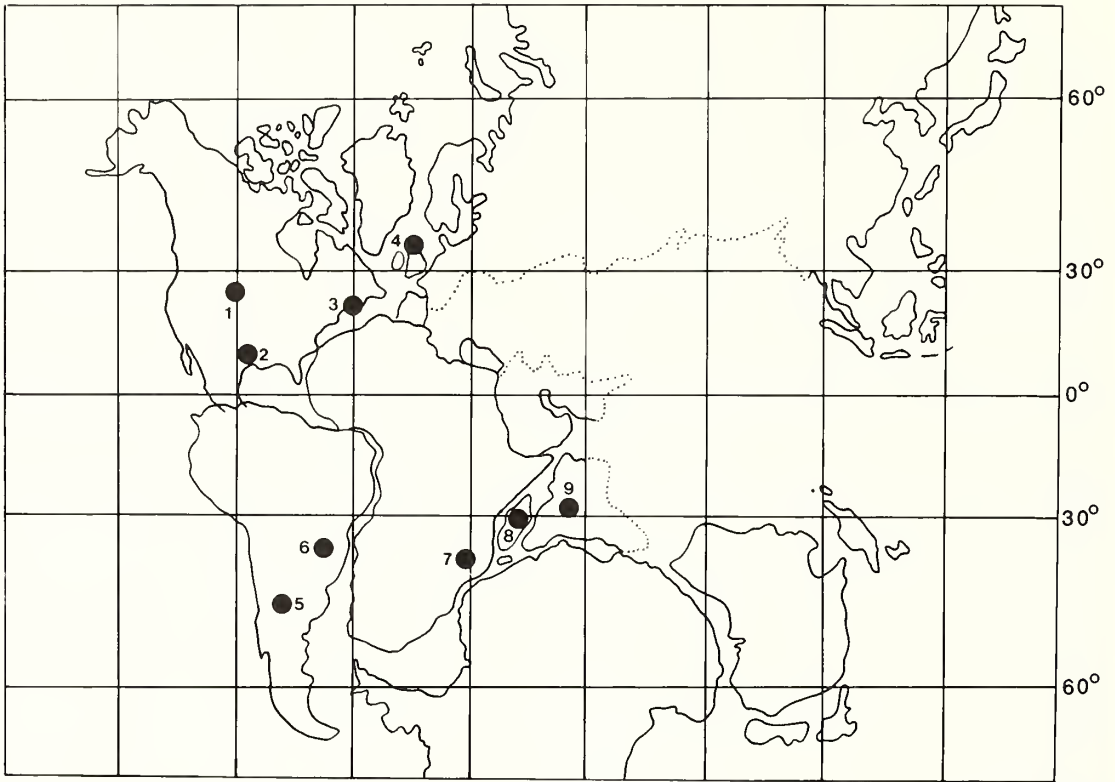
In 1976, Sankar Chatterjee identified a fragment of a rhynchosaur premaxilla (TMM 31185-92; Pl. 1, figs 2 and 3) in the collections of the Texas Memorial Museum from the lower Dockum Group near Otis Chalk, Texas (Elder 1978; Chatterjee 1980). Subsequently, Elder (1978) identified two humeri and two femora from a nearby locality, and another premaxillary fragment from the same locality, as pertaining to a rhynchosaur. Long (in Murry 1989) recently suggested that only the premaxillary fragments pertain to a rhynchosaur and that the postcranial bones represent a large trilophosaurid.

All but one of the putative rhynchosaur specimens were collected by workers employed by the Federal Works Progress Administration from 1940–1941 from the lower Dockum Group in Howard County in West Texas (Elder 1978; Murry 1989).

The putative rhynchosaur specimens include a 65 mm-long left premaxillary fragment (TMM 31185-92) which is very similar to rhynchosaur premaxillae in having the overall shape of a flattened, tapering cylinder, in having a flat internal margin in its distal half where the two premaxillae meet (Benton 1983*a*, p. 618) and in having longitudinal striations along its distal portion (Benton 1983*a*, p. 618). Thus, we consider that TMM 31185-92 is a rhynchosaur premaxilla. TMM 31185-93 is a 17 mm-long fragment also from quarry 3A, and it represents a portion of a premaxillary indistinguishable from TMM 31185-92.

All the putative rhynchosaur postcranial remains derive from quarry 1 and include two left humeri (TMM 31025-263, Pl. 1, fig. 1, Text-fig. 2; TMM 31025-262, Pl. 1, figs 4 and 5). These

RHYNCHOSAUR LOCALITIES



TEXT-FIG. 1. Distribution of Late Triassic rhynchosaurs: 1, Popo Agie Formation, Wyoming; 2, Dockum Group, Texas; 3, Wolfville Formation, Nova Scotia; 4, Lossiemouth Sandstone Formation, Scotland; 5, Ischigualasto Formation, Argentina; 6, Santa Maria and Caturrita Formations, Brazil; 7, unnamed unit, Tanzania; 8, Isalo II Beds, Madagascar; 9, Maleri and Tiki Formations, India.

humeri are very similar to rhynchosaur humeri (e.g. Huene 1929, pls 5, 6, 8; Huene 1942, pl. 34, fig. 4a-c; Chatterjee 1974, fig. 22a-d; Benton 1983b, fig. 49) in being very robust, with expanded ends linked by a narrow shaft with a proximal end consisting of a broad posterior plate and a narrow anteroventral deltopectoral crest, and with a distal articular surface divided into a large anterior capitellum and a large posterior trochlea. Thus, we consider that these humeri represent a rhynchosaur.

TMM 31025-266 is a reptilian femur which is very similar to rhynchosaur femora (Huene, 1938, pl. 10, 1a-f; Chatterjee 1974, fig. 25a-b; Benton 1983b, figs 33b-e and 51a-f) particularly in being robust, with moderately expanded ends, and in having a marked intertrochanteric fossa between two raised ridges on the proximal end, and in lacking a fourth trochanter. Thus, we consider that TMM 31025-266 represents a rhynchosaur. TMM 31025-264 appears to represent a deformed left femur of similar morphology.

In conclusion, it is apparent that a rhynchosaur is present in the lower Dockum Group of Howard County, Texas which is distinct from other Late Triassic rhynchosaurs and represents a

new taxon. The aims of this paper are: (1) to name and describe the new rhynchosaur from Texas; (2) to review the age relationships of all Late Triassic rhynchosaurs; and (3) to consider briefly their palaeoecology. TMM refers to the Texas Memorial Museum, Austin, Texas.

SYSTEMATIC PALAEOLOGY

Class REPTILIA Laurenti, 1768
 Subclass DIAPSIDA Osborn, 1903
 Order RHYNCHOSAURIA (Gervais, 1859) Osborn, 1903
 Family RHYNCHOSAURIDAE Huxley, 1887
 Genus OTISCHALKIA gen. nov.

Derivation of name. After the abandoned settlement of Otis Chalk, Howard County, Texas (Gregory 1945, fig. 1).

Type and only species. *Otischalkia elderae* sp. nov.

Type locality. Quarry 1, site 3, near Otis Chalk, Howard County, Texas (Elder 1978, fig. 7A–B).

Horizon. Lower Dockum Group (undivided), late Carnian (late Triassic), *Paleorhinus* biochron (Hunt and Lucas 1990).

Diagnosis. As for species.

Otischalkia elderae sp. nov.

Plate 1, figs 1–7; Text-fig. 2A–C

- 1978 ‘*Dockumensia beckerorum*’ Elder (unpublished), p. 66, figs 16A–B, 17A–B; 18A–C; Pl. 2, figs 1A–D and 2A–D, Pl. 3, figs 1A–D, 2A–B, 3.
 1980 Rhynchosaur, Chatterjee, p. 58.
 1986 Rhynchosaur, Murry, p. 120.
 1989 Rhynchosaur, Murry, p. 108.
 1990 Rhynchosaur, Benton, p. 84.

Derivation of name. For Ruth L. Elder who identified much of this rhynchosaur material.

Holotype. TMM 31025-263; left humerus (Pl. 1, fig. 1).

Referred specimens. TMM 31025-262, left humerus (Pl. 1, figs 4 and 5); TMM 31025-266, left femur (Pl. 1, figs 6 and 7); TMM 31025-264, left femur; TMM 31185-92, fragment of left premaxilla (Pl. 1, figs 2 and 3); TMM 31185-93, tip of premaxilla.

Diagnosis. *Otischalkia* differs from all rhynchosaurs except *Stenaulorhynchus* in having a hook on the supinator process of the humerus, and from *Stenaulorhynchus* in having a narrower proximal than distal end to the humerus, a much smaller and more discrete deltopectoral crest, and a larger capitellum than trochlea on the distal humerus.

Description. The left premaxillary fragment identified by Chatterjee from quarry 3A (TMM 31185-92; Pl. 1, figs 2 and 3) was described above. TMM 31185-93 is broken at both ends, but only a few millimetres are probably missing from the tapering distal end. TMM 31185-93 also tapers proximally.

The holotype humerus of *Otischalkia*, TMM 31025-263 (Pl. 1, fig. 1; text-fig. 2A–C), and the referred humerus TMM 31025-262 (Pl. 1, figs 4 and 5), are very similar in morphology. These humeri are relatively short and robust with greatly expanded ends, with an angle of torsion between the ends of about 55°, and a narrow shaft linking them. The proximal end consists of a broad posterior plate and a relatively broad anteroventral deltopectoral crest. The shaft is narrow and elliptical in cross-section. Like *Hyperodapedon* (Benton 1983b, p.

668), the distal end has a large anterior capitellum for articulation with the radius and a posterior trochlea for the ulna. The supinator crest above the ectepicondylar groove has a hook-like projection.

The femur of *Otischalkia* (Pl. 1, figs 2 and 3) is robust, with a relatively straight shaft, a well-developed intertrochanteric fossa and no fourth trochanter. TMM 31025-266 (Pl. 1, figs 6 and 7) is a robust femur with a relatively straight shaft. Proximally, the internal trochanter forms a broad projection, separated from a large ovoid articular surface by an intertrochanteric fossa. The distal articular surface is divided into two distinct condyles, both of which may have been for the tibia (Benton 1983b).

Discussion. The *Otischalkia* humeri differ greatly from the elongate gracile humerus of *Trilophosaurus* (Gregory 1945, Pl. 27, figs 1-3; *contra* Long, in Murry 1989). Although rhynchosaur humeri are conservative in their morphology, the Texas specimens differ from the humeri of other rhynchosaurs. The Texas rhynchosaur differs from *Hyperodapedon gordonii* in having a distal expansion of the humerus that is as wide as the proximal end, and from all Late Triassic rhynchosaurs in having a hook-like process on the supinator crest. The morphology of the supinator process in *Otischalkia* is very like that of the Middle Triassic *Stenaulorhynchus* which also has a hook on the supinator process (Huene 1938, pl. 7, fig. 3a-d). However, the humerus of *Stenaulorhynchus* differs from the Texas humeri in having a greatly expanded proximal end which is wider than the distal end, a much longer and narrow shaft between the expanded ends and in having a much larger capitellum than trochlea on the distal end (Huene 1938, pl. 7, fig. 3A-D; Pl. 1, figs 4, 5; Text-fig. 2A-C).

TMM 31025-266 is more gracile than femora of *Hyperodapedon* (Chatterjee 1974, fig. 25a-b; Benton 1983a, fig. 33b-e) and apparently differs from all other rhynchosaurs in having an internal trochanter that extends almost to the proximal articular surface, although this feature may be partly due to poor preparation. TMM 31025-266 is very different in morphology from *Trilophosaurus* femora (*contra* Long in Murry 1989) in: (1) being more robust; (2) not being strongly, longitudinally sigmoidal; and (3) in having less offset distal condyles (Gregory 1945, pl. 29, figs 5 and 6).

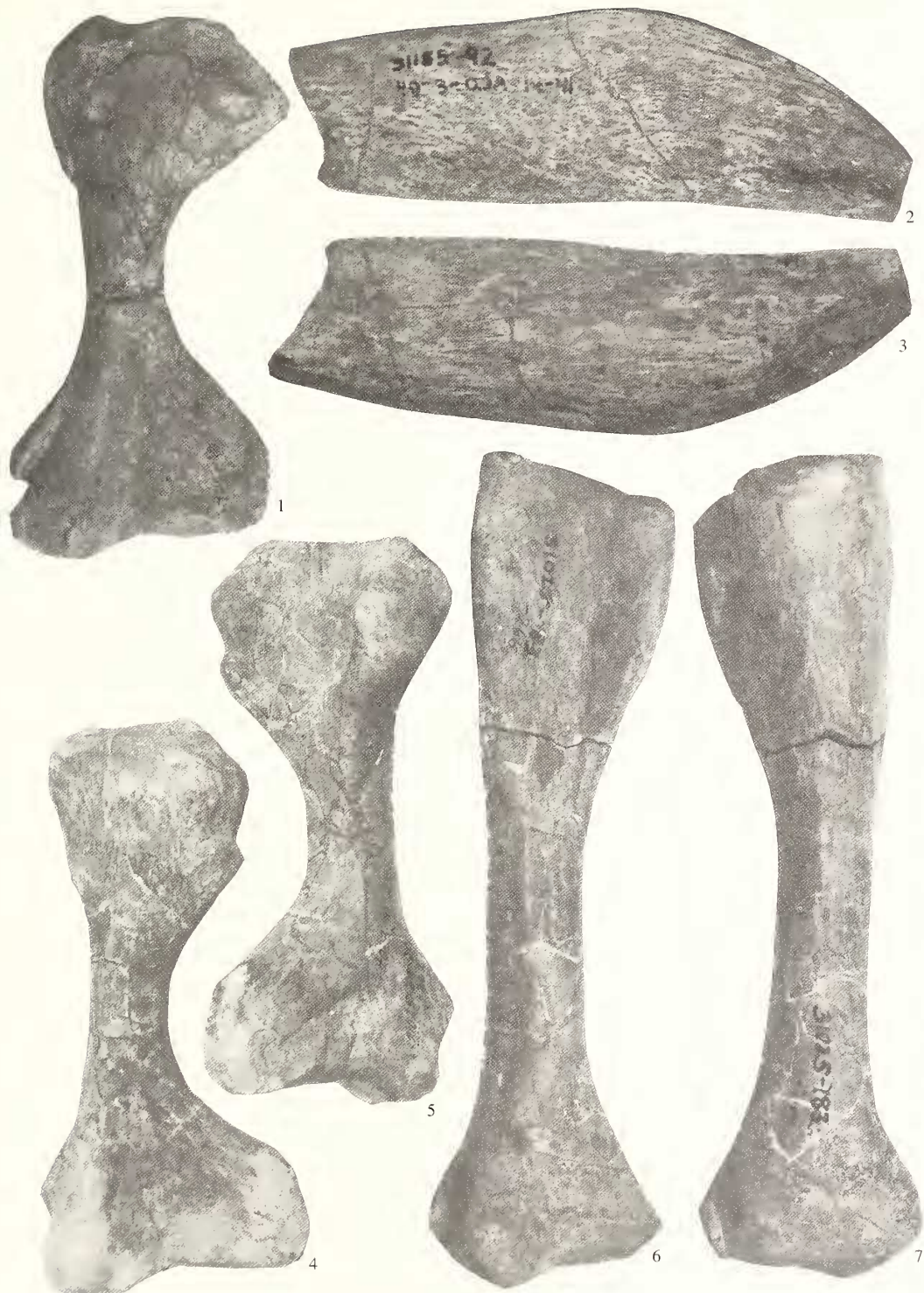
Lacking cranial material, it is not clear what subfamily this taxon belongs to. But, as all Late Triassic rhynchosaurs apparently pertain to the Hyperodapodontinae, we tentatively assign the Texas taxon to this subfamily.

LATE TRIASSIC RHYNCHOSAUR TAXONOMY AND DISTRIBUTION

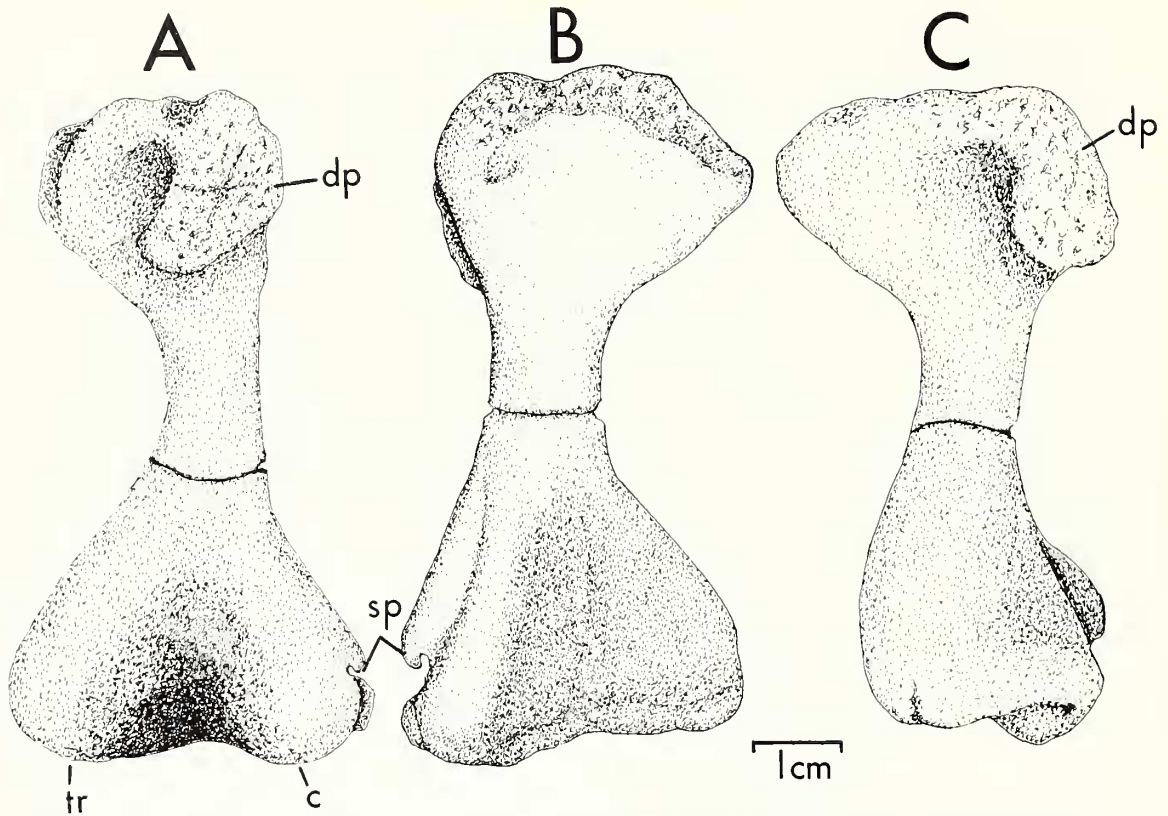
Western United States. Hotton (in Parrish 1989a, p. 362; 1989b, p. 237; Hotton oral comm., 1990) reports finding fragmentary remains of a rhynchosaur from the Popo Agie Formation, south of the Big Horn Mountains in north-central Wyoming. Parrish (1989a, p. 362; 1989b, p. 237) reported the presence of rhynchosaur bones from the *Placerias* quarry of northeastern Arizona in the lower Chinle Formation. R. A. Long (oral comm. 1990) believes that these specimens represent a large trilophosaur, but, pending publication of these specimens, we tentatively assume that they represent a rhynchosaur. Murry (1989) reported a 'rhynchosaur' in the Norian Redonda Formation in east-central New Mexico, but there is no evidence of any animal similar to a rhynchosaur in this assemblage (Hunt 1991).

EXPLANATION OF PLATE I

- Fig. 1. *Otischalkia elderae* gen. et sp. nov.; holotype left humerus (TMM 31025-263); dorsal view, $\times 0.65$.
 Figs 2 and 3. *Otischalkia elderae* gen. et sp. nov.; left premaxillary fragment (TMM 31185-92). 2, lateral view. 3, mesial view. Both $\times 1.9$.
 Figs 4 and 5. *Otischalkia elderae* gen. et sp. nov.; left humerus (TMM 31025-262). 4, dorsal view. 5, ventral view. Both $\times 0.65$.
 Figs 6 and 7. *Otischalkia elderae* gen. et sp. nov.; left femur (TMM 31025-266). 6, posterior view. 7, anterior view. Both $\times 0.65$.



HUNT and LUCAS, *Otischalkia elderae*



TEXT-FIG. 2. *Otischalkia elderae* gen. et sp. nov.; holotype left humerus (TMM 31025-263). A, posteroventral view. B, anterodorsal view. C, anteroventral view. Abbreviations: c, capitellum; d, deltopectoral crest; sp, supinator process; tr, trochlea.

Canada. Baird (1964) first mentioned rhynchosaur specimens from the Wolfville Formation of Nova Scotia, but they have never been adequately described. The presence of one longitudinal groove in the maxilla of the Wolfville specimens and the absence of lingual teeth on the maxilla (Chatterjee 1980) places them in the subfamily Hyperodapedontinae (Chatterjee 1969, 1974; Benton 1983*b*, 1987). The only member of this subfamily that lacks lingual dentition on the mandible (Chatterjee 1980), and a single tooth row on the dentary (Benton 1990), like the Wolfville taxon, is *Scaphonyx*. Thus, pending formal description, we assign the Wolfville specimens to *Scaphonyx* sp.

Brazil. Woodward (1907) named the rhynchosaur *Scaphonyx fischeri* from the Santa Maria Formation of Brazil. Huene (1926) erected several other taxa of rhynchosaurs from the Santa Maria but these have all been synonymised subsequently with *S. fischeri* (Huene 1942; Sill 1970). *Scaphonyx* is restricted to the 'Scaphonyx assemblage zone' of the upper Santa Maria Formation (Barberena *et al.* 1985). Barberena *et al.* (1985) also reported the discovery of a probable new species of *Scaphonyx* in the Caturrita Formation which overlies the Santa Maria, but the specimens have not been described.

Argentina. Sill (1970) described specimens from the Ischigualasto Formation of western Argentina as *Scaphonyx sanjuanensis*. *S. sanjuanensis* is only slightly different from the better known *S. fischeri* and may be synonymous (Benton 1987).

Scotland. All rhynchosaur specimens from the Lossiemouth Sandstone Formation of eastern Scotland are referable to the hyperodapedontine *Hyperodapedon gordonii*, which has been the subject of many articles, the last of which is an extensive monograph by Benton (1983b).

Morocco. Dutuit (1976) described *Acrodenta iredhi* from the middle of the Argana Formation in Morocco as a possible rhynchosaur, but this taxon is now considered to be captorhinid (Dutuit pers. comm. 1990).

Tanzania. Boonstra (1953) named two species of rhynchosaur, *Scaphonyx stockleyi* and *S. africanus*, from an unknown locality in the Tunduru district of what is now Tanzania. Chatterjee (1980) erected the genus *Supradapedon* for *S. stockleyi*. We agree with Benton (1983b, p. 712) that *Supradapedon* could be a large *Scaphonyx* or *Hyperodapedon*, and we refer *Supradapedon* to Hyperodapedontinae indeterminate. The holotype of *Scaphonyx africanus*, which is the proximal third of a weathered femur, is indeterminate, and thus this taxon is a *nomen dubium*.

Madagascar. Buffetaut (1983) named *Isalorhynchus genovefae* for a rhynchosaur maxilla from the Isalo II Beds which lacks lingual dentition. It is characteristic of the Hyperodapedontinae that they lack lingual teeth on the maxilla (Benton 1983b). The Madagascar genus contains only one species whose holotype is not diagnostic below the subfamily level (Benton 1987).

India. Huxley (1869) referred rhynchosaur tooth plates from the Maleri Formation to *Hyperodapedon gordonii*. Feistmantel (1880) mentioned the occurrence of rhynchosaurs in the Tiki Formation. Lydekker (1881) named these specimens *Hyperodapedon huxleyi*, and Huene (1938) erected the genus *Paradapedon* for this species. Benton (1983b) concluded that the Indian rhynchosaur should be considered a species of *Hyperodapedon*, *H. huxleyi*.

PALAEOECOLOGY OF LATE TRIASSIC RHYNCHOSAURS

Rhynchosaurs had a cosmopolitan distribution during the Late Triassic (Text-fig. 1), but their relative abundance varies considerably between faunas. Faunas rich in rhynchosaurs (Santa Maria, Ischigualasto, Lossiemouth Formations) all occur in Gondwanaland with the exception of the Lossiemouth, and contemporaneous faunas depauperate in rhynchosaurs (lower Dockum, Popo Agie, Chinle, Wolfville Formations) all occur in Laurasia. This distribution corresponds to two broad palaeobotanical provinces, characterized in the south by the *Dicroidium* flora and in the north by a 'cycadophyte'/fern/conifer flora (Tucker and Benton 1982; Benton 1983a; Olsen and Galton 1984). However, it should be noted that, except for Lossiemouth, in Laurasia, faunas rich in semiaquatic phytosaurs and metoposaurs, represent different facies than the southern Gondwanaland faunas dominated by terrestrial animals (Benton and Walker 1985). Thus, we would expect the semiaquatic and more terrestrial facies to produce different floras. Thus, although we recognise that there are two different provinces in the Late Triassic, we believe that many differences between the northern and southern faunas are ecological in nature as previously suggested (e.g. Benton 1983a; Benton and Walker 1985). In strong support of this notion, we note the recent recognition of characteristic elements of the southern faunas in Laurasia. These include the occurrence of *Scaphonyx* in the Wolfville Formation of Nova Scotia and other rhynchosaurs in Wyoming, Texas, and Scotland, the dicynodont *Ischigualastia* in the Santa Rosa Formation of New Mexico (Lucas and Hunt 1991), the ictidosaur *Pachygenelus* in the Cooper Formation of Texas (Chatterjee 1983), and a southern-Gondwana-aspect fauna in Virginia (Olsen 1989b).

BIOCHRONOLOGY OF LATE TRIASSIC RHYNCHOSAURS

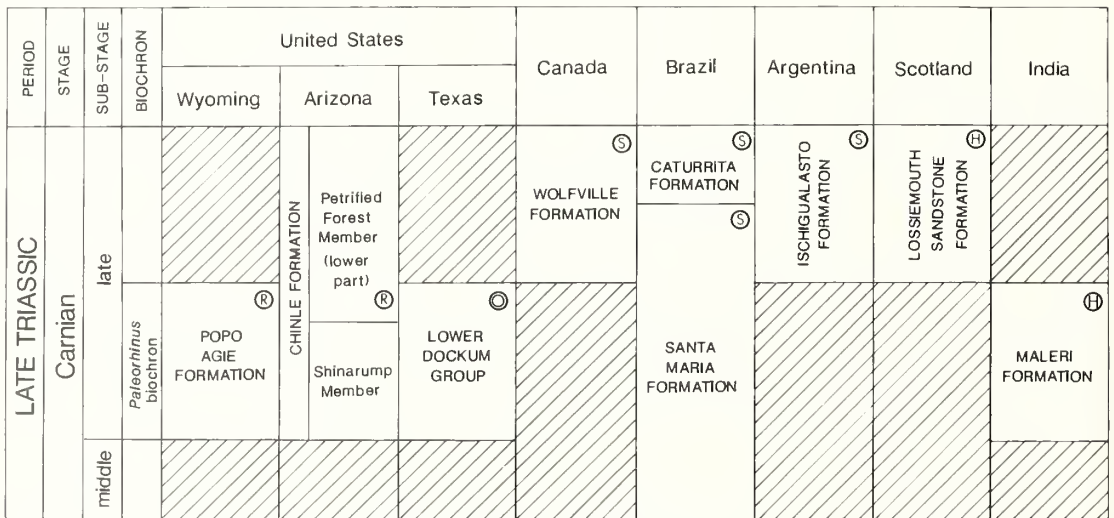
Prior to the 1970s, several of the rhynchosaur-bearing formations, principally those in South America, that we now consider to be Late Triassic in age, were assigned to the Middle Triassic

(Romer 1962, 1966, 1970). However, now all the rhynchosaur-bearing formations reviewed above are considered to be late Carnian in age (e.g. Olsen and Sues 1986; Text-fig. 3) or possibly early Norian (Benton and Walker 1985). Our review of the evidence for the age of Late Triassic rhynchosaurs indicate they are all of probable late Carnian age.

Two of the rhynchosaur records discussed above are from stratigraphic units with poor age control. The hyperodapedontine from Tanzania was collected from beds of unknown age (Boonstra 1953), which have subsequently been assigned to the ?Upper Triassic because of the presence of the rhynchosaur (Chatterjee 1980). The Madagascan hyperodapedontine is from the Isalo II beds (middle Isalo Group; Buffetaut 1983) which have been considered Rhaetic (on the basis of phytosaurs and metoposaurs) to Liassic (on the basis of ammonites) in age (Besaire and Collignon 1960; Guth 1963; Westphal 1970; Dutuit 1978). However, the presence of unidentifiable phytosaurs and metoposaurs in the lower part of the unit gives no greater age precision than Late Triassic. Buffetaut (1983) suggests that the rhynchosaur from the basal beds of Isalo II is a rhynchosaurine and thus of Middle Triassic (Ladinian) age. Furthermore, the Isalo rhynchosaur is a hyperodapedontine (Benton 1987) and thus is probably of Late Triassic age, which is in agreement with other faunal evidence for the age of these beds.

Four of the remaining occurrences of Late Triassic rhynchosaurs are from faunas that contain the phytosaur *Paleorhinus* (Popo Agie, Chinle, lower Dockum and Maleri). *Paleorhinus* is important to Late Triassic biochronology because it is the only terrestrial vertebrate also known from marine strata and thus provides a means of correlating terrestrial faunas directly to marine stages (Huene 1939b; Hunt and Lucas 1991). The *Paleorhinus* specimen from marine strata is from the Opponitzer Beds near Lunz in Austria which are of Tuvallian (late Carnian) age (Janoscheck and Matura 1980; Zapfe written comm. 1989). Thus, in the absence of any conflicting data we assign all *Paleorhinus*-bearing strata to the *Paleorhinus* biochron of late, but not latest, Carnian age (Hunt and Lucas 1990). Pollen data, where available, support these age assignments (Dunay 1972; Dunay and Fisher 1979; Kumaran and Matheswari 1980; Litwin 1986). This means the rhynchosaur occurrences in the Popo Agie, lower Dockum, lower Chinle, and Maleri are of late Carnian age.

The faunas of the Ischigualasto Formation of Argentina and the upper Santa Maria Formation of Brazil share several taxa in common, including *Scaphonyx*, the aetosaur *Aetosauroides* (Casamiquela 1960; Barberena *et al.* 1985), and the dinosaur *Staurikosaurus* (Colbert 1970; Brinkman and Sues 1987). Faunal differences between these two units include the presence of



Ⓜ Hyperodapedon Ⓞ Otischalkia Ⓢ Scaphonyx Ⓡ undescribed/undiaagnostic rhynchosaur

TEXT-FIG. 3. Correlation of Upper Triassic rhynchosaur-bearing strata.

herrerasaurs and an ornithischian in the Ischigualasto and more specimens of therapsids in the Argentinian than Brazilian strata (Barberena *et al.* 1985). These differences are probably ecological in origin and thus there appears to be no basis for the widely held belief that the Santa Maria as a whole is slightly older than the Ischigualasto (e.g. Sill 1969; Benton 1988). The Caturrita Formation, which overlies the Santa Maria Formation in Brazil, shares *Proterochampsa*, *Scaphonyx*, and *Exaeretodon* with the Ischigualasto (Barberena *et al.* 1985). It appears that the Caturrita represents a more Ischigualasto-like facies than the upper Santa Maria, and that both are age equivalents of parts of the Ischigualasto Formation of Argentina (Barberena *et al.* 1985, fig. 8). These formations are usually considered ?middle-late Carnian in age (e.g. Benton 1988). There are however, problems in correlating these faunas with those of Laurasia and northern Gondwanaland because of marked ecological differences. The northern faunas, which are dominated by semi-aquatic tetrapods, have been referred to the metoposaur/phytosaur empire and the southern faunas, which are dominated by terrestrial tetrapods, to the rhynchosaur/diademodontid empire (Tucker and Benton 1982; Benton 1983a). However, we believe that there is growing evidence that the Brazilian and Argentinian faunas, containing rhynchosaurs, are of late Carnian age. Lucas and Hunt (1991) recently recognised the dicynodont *Ischigualastia* from post-*Paleorhinus* biochron strata of late Carnian age in New Mexico. This taxon is otherwise restricted to the Ischigualasto Formation. Late Carnian (post-*Paleorhinus* biochron) strata in the American Southwest also include staurikosaurid dinosaurs similar to *Staurikosaurus* from the Ischigualasto and Santa Maria Formations (Murry and Long 1989; Hunt and Lucas 1989; Hunt 1990). In addition, we recognise the rhynchosaur *Scaphonyx* in the Wolfville Formation of Nova Scotia which is also late Carnian in age (Olsen 1989a). *Scaphonyx* also occurs in the Ischigualasto, Santa Maria, and Caturrita Formations. Thus, we consider that these South American formations are of late Carnian age, based on the evidence of the distribution of *Ischigualastia*, *Scaphonyx*, and staurikosaurids.

However, to refine the age of the Ischigualasto, Santa Maria, and Caturrita Formations, we must further consider the age of the Wolfville Formation. The Wolfville fauna (Baird and Olsen 1983; Olsen 1989a) includes taxa known elsewhere from the *Paleorhinus* biochron in Texas ('*Metoposaurus*' *bakeri*) and from post-*Paleorhinus* biochron, late Carnian strata of the American Southwest (cf. *Stagonolepis*). There are no pollen (Traverse 1983) or other data to constrain further the age of the Wolfville. However, as the *Ischigualastia* occurrence in New Mexico is in undoubtedly post-*Paleorhinus* strata, we believe that it is probable that all *Scaphonyx*-bearing strata (Wolfville, Ischigualasto, Santa Maria, Caturrita) are of post-*Paleorhinus* biochron age.

The age of the Lossiemouth Sandstone Formation of Scotland has been the subject of debate (Benton and Walker 1985; Olsen and Sues 1986). At the generic level, the Lossiemouth shares *Hyperodapedon* with the Maleri Formation (Benton 1983b) of the *Paleorhinus* biochron and *Stagonolepis* with post-*Paleorhinus*, late Carnian strata of the American Southwest (Walker 1961; Murry and Long 1989). In addition, the Lossiemouth shares the procolophonid *Leptopleuron* with the Wolfville (Baird and Olsen 1983), possibly at the specific level (Olsen and Sues 1986). We thus tentatively refer the Lossiemouth to a post-*Paleorhinus* biochron (late Carnian) age based on the procolophonid correlation with the Wolfville.

In conclusion, all Late Triassic hyperodapedontine rhynchosaurs that can be dated with any accuracy are of late Carnian age (Text-fig. 3). The faunas that contain rhynchosaurs are both of *Paleorhinus*-biochron and post-*Paleorhinus*-biochron age. *Scaphonyx* is restricted to post-*Paleorhinus* biochron (Wolfville, Santa Maria, Caturrita, Ischigualasto) strata whereas *Hyperodapedon* occurs in both *Paleorhinus*-biochron (Maleri) and post-*Paleorhinus*-age strata (Lossiemouth).

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